THE EXCRETORY AND CIRCULATORY SYSTEMS OF CRYPTOCHITON STELLERI MIDD.

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Somewhat over half a century ago Middendorff ('49) published his extensive studies on the anatomy of *Cryptochiton stelleri*, the largest and in some respects the most highly modified of the chitons. In several important details this was a decided contribution to our knowledge of the group and yet the work has not received the attention it has merited chiefly for the reason that the facts are inextricably associated with numerous errors (due to poorly preserved material) and are illustrated by figures often difficult to interpret. It is the purpose of the present paper to explain and to a certain extent correct Middendorff's results and especially to describe some of the more noteworthy features of the excretory and circulatory systems. This latter disvision of the subject may appear unnecessary owing to the extensive chiton studies already published, notably those of Haller ('82), Pelseneer ('99), Thiele ('02), and especially Plate ('97), but as will be noted in the following pages this species differs in several fundamental particulars from any other known form.

The specimens on which Middendorff's studies were based came from the shores of Kamchatka and from that locality this species extends to the southward fully 2,500 miles, the southern limit being approximately Monterey Bay, California. Throughout the greater part of their range, as I know from personal observation, they are confined to the littoral zone, rarely extending into water more than three fathoms in depth. Usually they are more or less concealed among the red algæ (especially *Gigartina exasperata*) upon which they feed and with which they harmonize so closely that they escape the untrained eye. While the largest northern specimens in my possession measure less than 20 cm. (8 inches) in length, some in the vicinity of San Francisco not infrequently are 25 cm. (10 inches) long. The largest specimen I have ever seen measured slightly more than

33 cm. (13 inches) when alive and in a resting condition and weighed seven grams less than two kilograms (4.4 lbs.).

Regarding the breeding habits little may be said at the present time. On three different occasions I have found males shedding their sex products in the latter part of February and at this time the females are distended with eggs. The oviduct is provided with an albumen gland in all essential respects like that of *Ischnochiton magdalenensis* (Heath, '99) and it is reasonable to suppose that like this last-named species *Cryptochiton* lays its eggs imbedded in a gelatinous envelope. In the early part of the summer the young have attained a length of from 10 to 22 mm., and as has been described in a previous paper (Heath, '97) the shells are still exposed. The mantle of these small individuals is usually of a yellow or orange color, exceptionally light green, and is beset with more or less definitely arranged yet scattered groups of crimson spicules characteristic of the adult. As these increase in number the general shade ordinarily changes to a brick red[1] not infrequently blotched with patches of white or purplish-white that usually disappear by the time the animal has become sexually mature.

Middendorff was the first to discover the kidney in the chitons yet it was with some hesitancy that he applied this name to it, as his observations were very incomplete. However, it must be said they are more perfect than some of his critics have supposed. He correctly states that the excretory canals unite in front of the pericardium in "einem geschlossenen Bogen" (p. 73) and he accurately locates the glandular portion, but the fact was never discovered that this latter division is penetrated by two canals, one of which connects with the pericardium while the other opens to the exterior.

The kidney holds the usual position at the sides of the visceral cavity and posseses the form of a very slender U, the free extremities terminating in the reno-pericardial, and external openings, while the opposite rounded end is situated at the level of the anterior margin of the third valve of the shell (Fig. 1).

[1] Middendorff described his specimens as yellowish brown but this was due to the fact that the tufts of bristles had been worn away exposing the mantle to an abnormal degree.

At the extreme lateral border of the percardium and about one fourth its greatest length from its anterior end the relatively large inner opening occurs (Fig. 2, *r*) and almost immediately leads into a flat disc-like cavity closely attached to the ventral pericardial wall. From the inner border of this flattened sac a slender delicate tube, usually almost invisible in preserved material, proceeds forward and becomes continuous with the more dorsal tube of the glandular portion of the kidney proper. This last-named section consists, as in chitons generally, of numerous highly branched lobules which extend ventrally some distance on the inner surface of the foot, dorsally to the valves of the shell and to the head cavity in front.

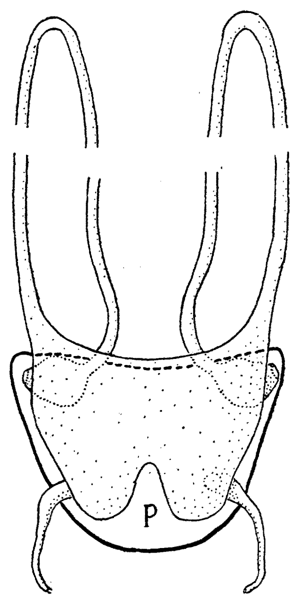


Fig. 1. Diagram illustrating the kidney of *C. stelleri*, ventral view; *p*, pericardium.

In a number of species of chitons the outer limb of the excretory canal expands into a well defined reservoir (Nierensack), which is also supplied with glandular outgrowths. In some cases these reservoirs are of comparatively large size and in a few cases they may extend close to the mid-line, but here, as in every species of chiton hitherto described, one kidney is wholly independent of the other. In *Cryptochiton*, on the other hand, the reservoirs, that are probably distinct in very young specimens, unite in the mid-line and form, as Figs. 1 and 2 show a spacious chamber lying ventral to the anterior third of the pericardial cavity. In specimens one fourth the adult size, and occasionally in individuals of much greater length, there are slight indications of a median partition that may represent the line of fusion of the once independent divisions.

Carefully removing the rectum and opening the ventral wall of this common reservoir the latter will be found to terminate posteriorly in two triangular diverticula, each of which communicates by means of a narrow slit immediately behind the trans-

verse blood sinus (sinus transversus) with a dorsal disk-like cavity in contact with the ventral pericardial wall (Fig. 2). From the antero-lateral border of each of these last-named spaces a slender tube arises and passing outward plunges beneath the afferent branchial sinus and then curving backward gradually approaches the surface of the body and opens through the renal papilla. The position of the external excretory opening is, unlike that of the genital papilla, remarkably constant in position. In one hundred specimens examined on this point the excretory

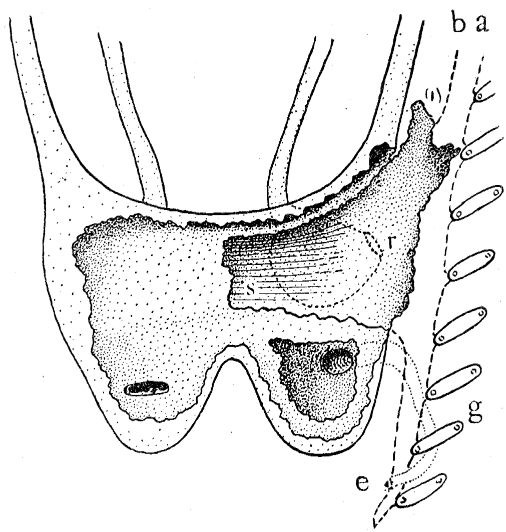


Fig. 2. Posterior part of kidney of *C. stelleri*. The ventral wall has been removed and a portion of the dorsal in order to show the transverse sinus (*s*) and the exit of the ureter; *ba*, branchial artery; *e*, outer kidney opening; *g*, gill; *r*, renal pericardial opening; genital opening opposite eighth gill.

pores were, with a very few slight exceptions, situated opposite the last gill.

Connective tissue cells laden with concrements, such as were described by Brock ('83) for several molluscs, are present in *Cryptochiton* in great abundance. In all specimens, but notably those above 10 cm. in length they form great accumulations in the foot and mantle in the vicinity of the mantle furrow and give the tissue the appearance of having been charged with light yellow sand which cuts with a distinctly gritty sound. Cells of this

character are distributed to a greater or less extent throughout the entire foot and mantle but sooner or later they make their way to the main accumulations by means of amœboid movements and possibly through the agency of the blood stream. In the young of several species of chitons (less than 1 mm. in length) these concrement bearing cells may be seen to originate from the mesenchyme elements that also form the connective tissue, blood and apparently some of the muscle elements. The concrements arise in the form of one or two small refringent granules in each cell and gradually increasing in size and usually in number sooner or later almost completely fill the cell which during this period usually takes up a position near some blood sinus. In the description of the circulatory system attention is called to the fact that a large blood sinus (lateral sinus) with numerous branches penetrates these "Granulazellen" but the relation of the two remains uncertain. Sections not infrequently give the impression that these cells passing into the sinus disintegrate after which the resulting products may be taken up by the kidney but there is no definite assurance that such is the case.

There are only two papers in which a serious attempt has been made to trace the circulation of the blood in the chitons. The first by Middendorff is very incomplete and in many respects incorrect; while the second by Plate is much more detailed yet in certain fundamental particulars, it is not in accord with the results set forth in the following paragraphs.

As we know from the work of Middendorff the heart in this species is essentially the same as in other chitons consisting as it does of a median ventricle and the lateral auricles. This author however made the mistake of claiming that these latter chambers end blindly behind (for they are united in the usual fashion) and that the ventricle gives off numerous small branches in the median ventral line to the rectum and laterally to the mantle edge and last valve of the shell. The supposed openings in this region are merely the depressions marking the attachment of delicate muscle fibers (trabeculæ carneæ) that span the cavity of the ventricle. In the auricles the same depressions appear but as injections clearly show the only blood, besides that from the efferent branchial sinus, that enters these chambers comes from the mantle at

the extreme posterior end of the animal through two small vessels close to the mid-line behind and in certain cases even these openings appear to be absent.

The relations of the aorta to the heart and head cavity and the origin of the genital arteries Middendorff correctly determined but the account of the last-named vessels is somewhat obscure. A careful examination shows that they course between the folds of the inner wall of the gland very much as in *Acanthopleura echinata* (Plate) and after branching repeatedly (and often not dichotomously) become lost among the developing sex products.

Concerning the course of the blood from the gonad I have nothing to add to Plate's account of *Acanthopleura echinata* except that in *Cryptochiton* a relatively large quantity leaves from the neighborhood of the gonoducts and enters the extensive sheets of kidney tissue adjoining the front end of the pericardium. From here very little blood appears to go into the visceral cavity but penetrating the spongy tissue of what may be termed the lateral space (Seitenlückenraum, Midd.; Lateralkammer, Plate) is poured into the lateral sinus (Seitenarterie, Midd.).

The dorsal arteries, lateral vessels between the II–V valves, supply some of the shell muscles in the fashion accurately described by Plate. Owing probably to the greater size of the mantle in *Cryptochiton* the intersegmental arteries are more numerous and of larger size than in other species of chitons. They arise sometimes singly (dividing almost at once) though usually in pairs from the dorsal side of the aorta between each valve and as well defined vessels may be traced for considerable distances. Usually these vessels do not extend far into a neighboring "segment" but in all of the specimens carefully examined on this point the vessels between segment V–VI are invariably of large size and extending latterly and posteriorly supply the greater part of the hinder portions of the mantle. The blood returning from the pallium pours into the lateral sinus.

Middendorff (p. 70) states that these small vessels (called by him Mantelarterien) appear to end blindly in the leathery substance of the mantle and on the other hand to open into the lateral sinus and the branchial artery. Plate also makes the statement that in *Acanthopleura echinata* most if not all of the

blood from the mantle passes into both the branchial artery and the branchial vein. In *Cryptochiton* the vessels from the mantle are of comparatively large size and may be followed without difficulty into the lateral sinus. Injections of the branchial artery and the branchial vein give no indication that they receive any blood directly from the mantle.

The marginal vessel (Randgefäss) imbedded in the mantle to the outside of the mantle furrow, a position corresponding to the lateral fold (Lateralfalte) of other chitons, is but a system of irregular sinuses supplied by vessels from the intersegmental artery. The blood returning from it passes, together with other blood from the mantle, into the lateral sinus.

In *Cryptochiton* the course of the blood leaving the head cavity is considerably different from that in any other chiton hitherto described. According to several investigators the blood leaves the head sinus by the following vessels: the visceral artery, the lateral sinus of the foot, vessels passing into the snout (Mundscheibe) and by means of canals surrounding the pedal and pallial nerves. In *Cryptochiton* no blood makes its direct exit by either the pedal or pallial neural sinuses and the course of the blood passing into the snout is considerably different from that described by Plate for *Acanthopleura echinata*, and furthermore there is a pair of pallial arteries.

The head cavity in the chitons is a comparatively narrow space surrounding the buccal mass and separated from the visceral cavity by a septum. Among the more important arteries leading out from it are two of large size which spring from the postero-lateral borders of the snout (Fig. 3). Almost immediately each divides, the inner branch, the pedal sinus, passing into the foot, the outer canal, the pallial artery, following along the mantle cavity in close proximity to the pallial or lateral nerve. The pallial sinus shortly after its origin gives off a branch which ramifies throughout the tissue of the proboscis supplying with its fellow all of the region behind the mouth. It is also in communication with an extensive sinus encircling the snout as will be described presently. By means of injections each pallial sinus may be followed into the region of the reproductive opening where, after having gradually diminished in size, it vanishes com-

pletely. Delicate branches supply the tissue of the immediate region, some going to the lateral nerve another portion to the tissue of the lateral space and it is possible that another quantity though very small may enter the adjacent regions of the mantle.

Middendorff (pp. 69, 70) speaks incorrectly of two pairs of vessels which arise from the head cavity and passing in close proximity to the mantle furrow open into the sinus transversus (arcus arteriosus). In *Cryptochiton* the only vessel which

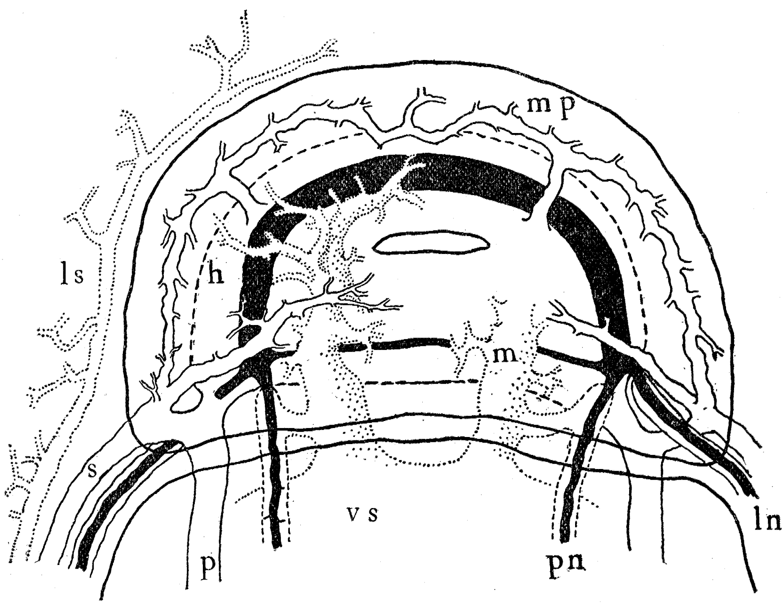


Fig. 3. Diagram illustrating the circulation of snout and certain vessels leaving the head cavity in *C. stelleri*. *h*, head cavity; *ln*, lateral nerve sinus; *ls*, lateral sinus; *m*, median proboscis protractor; *mp*, marginal proboscis protractor; *p*, pedal sinus; *pn*, pedal nerve sinus; *s*, pallial sinus: *vs*, visceral cavity; nervous system, black.

holds such a position posteriorly is the lateral sinus and this as is well known has no connection whatever with the head cavity, and on the other hand the pallial artery connects with the head cavity but does not communicate with the transverse sinus.

Heretofore it has been held that the sinuses surrounding the pallial cords conduct a considerable amount of blood from the head cavity into the mantle but in not less than 50 specimens of *Cryptochiton* injections from the head sinus failed to penetrate

these canals and dissections show that at or near the point of union of the pallial and pedal cords a connective tissue and muscular septum (Fig. 3) completely separates the nerve sinuses from the head cavity. However a short distance behind this point and throughout the greater part of the succeeding portions of the mantle furrow there are frequent communications between the pallial and nerve sinus so that this latter space and adjacent regions are probably filled in life with comparatively pure blood.

In *Cryptochiton* another part of the blood passing out of the head cavity enters the proboscis or snout chiefly by means of two large vessels located on each side of the mid-line about level with the mouth (Fig. 3). Almost immediately these break up into two or three branches that pass outward to the margin of the proboscis where they become continuous with an extensive system of spaces forming a semicircular vessel (*mp*) coextensive with the margin of the snout. From this marginal sinus smaller vessels pass inward and furnish fresh blood to the proboscis tissue, while another supply of arterial blood, much smaller in amount, passes into the snout through sinuses surrounding the nerves. As the figures indicate no part of the blood from any of these sources passes into the tissue of the foot, at least not in any appreciable quantity, but is conveyed along the region of the mantle furrow by means of the relatively large pallial sinus leaving the proboscis at its outer posterior angle, or it may be passed into the visceral cavity as described presently.

Middendorff figures (*f′*, Fig. 2, Pl. VIII.) a small curved canal which surrounds the snout anteriorly and states (p. 72) that it lies between the external and internal oral sphincter. Owing to the fact that in one specimen he was able to force the injection mass from the branchial artery into this vessel he considered it to be the anterior union of the branchial arteries but as these latter vessels certainly do not extend much farther forward than the most anterior gill and have no direct connection with the proboscis, I am of the opinion that the connections as described are incorrect and that the marginal vessel is the same one shown in Fig. 3.

Not only are the margins of the proboscis capable of considerable expansion owing to the influence of an abundant blood sup-

ply but as may be seen in living specimens the more central portions bounding the mouth are likewise subject to great distension. This is produced by a system of vessels present also in *Acanthopleura echinata* according to Plate though their connections are considerably different. From the extreme anterior and ventral part of the visceral cavity they arise as two relatively very wide canals one on either side of the mid-line. Coursing almost directly forward they enter the proboscis and giving off vessels into the more superficial portions encircle the mouth almost to the mid-line in front. Upon the contraction of some of the more anterior pedal muscles the visceral cavity is decreased in volume and a portion of the blood coursing through spaces in the region of the stomach is forced into the proboscis resulting within a short time in a marked increase in size and roundness of its central portions. In recently killed specimens pressure on the front part of the foot produces this phenomenon.

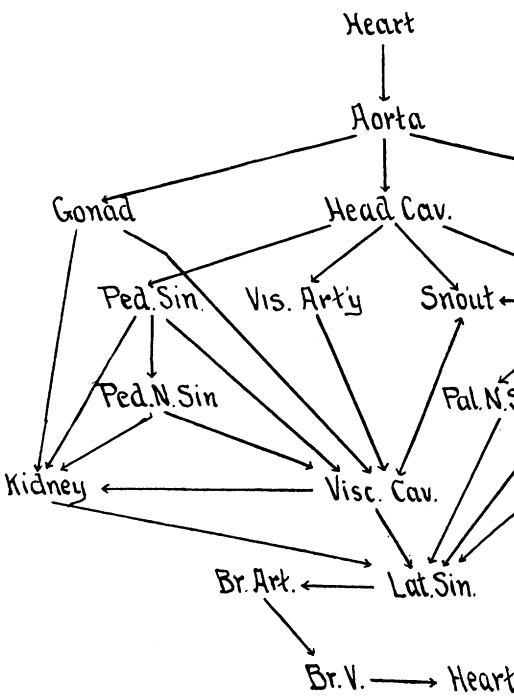
From injections it appears very probable that a considerable portion of the venous blood from the snout, when this is not protruded, passes into the visceral cavity by means of these protractor sinuses. The marginal portions of the proboscis and possibly the more central regions also are relieved of a portion, seemingly small, of their blood supply by means of several highly branched vessels emptying into the lateral sinus external to the snout.

In *Acanthopleura echinata* according to Plate the foot is provided with a median sinus which anteriorly connects with two vessels surrounding the mouth and corresponding to the median proboscis protractors of *Cryptochiton*. Were these latter vessels in *Cryptochiton* to be separated with a portion of the visceral cavity and fashioned into a median pedal sinus the relations would be essentially the same as in the above-named species. However the course of the blood leaving the median sinus is not by the usual exit from the visceral cavity for Plate states that it passes into the branchial artery.

The blood enters the foot by the two pedal sinuses, whose relations are already known, and leaves by two routes — into the visceral cavity or along the transverse pedal muscles to the kidney. As has been shown the contraction of some of the anterior pedal muscles may drive a quantity of blood into the proboscis, thus

causing its protrusion, and it is reasonable to suppose that according to the state of contraction of the pedal muscles generally the blood pressure of the visceral cavity may vary, causing a flow of blood from the foot into the cavity or in a reverse direction. Injections show that in dead or flaccid animals the line of least resistance is from the pedal sinuses laterally into the kidney.

As with the pedal nerve sinus a well-defined septum destroys any communication with the head cavity (Fig. 3) but throughout its entire course it is in frequent communication with the pedal



sinus which supplies it and the adjacent regions with aerated blood.

In all of the specimens carefully examined a connection exists between the pedal nerve sinus and the bases of the median protractor sinus (*m*) so that blood may pass from one to the other. Throughout its greater extent the pedal nerve sinus receives its blood from the pedal sinus and it is difficult to understand this peculiar anterior connection unless it is some device to aid in the protraction of the anterior margin of the foot.

Middendorff correctly describes the visceral artery which springs from the head cavity and surrounding the radula sac supplies the alimentary canal and liver. The blood passing from the capillaries pours into the visceral cavity and joining that from the foot, proboscis and gonad proceeds through the meshes of the kidney to enter the lateral sinus.

The lateral sinus in *Cryptochiton* is a relatively large canal surrounded by connective tissue and muscle fibers in whose wide meshes are vast numbers of "granulazellen." Anteriorily it arises near the mid-line in the furrow surrounding the snout from which it receives a few small vessels while numerous others of large size drain the blood from the mantle. Coursing backward and constantly increasing in size it continues to receive vessels from the mantle and finally in the vicinity of the reproductive opening it unites with the branchial artery.

The accompanying diagram will serve to illustrate the course taken by the blood in passing through the body, at least it represents the main canals. It will be seen that the well-developed lateral sinus plays an important part, acting as a collector for the blood from all parts of the body and possibly its surrounding walls serve to remove certain wastes before being passed to the branchial artery.

The relations of the branchial artery and the branchial vein to the gills and the connections of the latter vessel to the heart are already well known and require no further comment.

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